



Flight Control in Complex Environments

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1. Summary

The **ultimate goal** of this project was to develop a model of a flight control strategy that is effective in simple as well as complex environments. Through a series of behavioural and anatomical investigations, we have made much progress in elucidating the flight control strategies and visual specialisations that allow insects, with their miniature brains and limited sensory systems to fly safely through cluttered natural environments. The most significant findings have been that the tropical orchid bee uses a novel brightness-based strategy to guide its flight in clutter. This strategy is computationally simple and efficient and not only allows orchid bees to avoid collisions when flying through a rainforest, it also allows them to locate apertures that are sufficiently large for them to fly through. Another important discovery that we have made during this project is that the three simple eyes, or ocelli of orchid bees have more than one function. Using the state-of-the-art micro computed tomography analyses of the ocelli, advanced 3D reconstruction techniques and ray tracing – all methods developed as part of this project – we were able to reconstruct the visual fields of these eyes. We discovered that each eye not only has a field of view focussed on the horizon, indicating a role in horizon stabilisation, they also have a large dorsal field of view that overlaps in all three eyes and appears to function as an analyser of polarised light. Overall, the findings of this project provide new insights into how insects control their flight and avoid collisions in complex environments. These insights are also relevant for the development of lightweight guidance systems that would enable autonomous aircraft to navigate heavily cluttered environments simply and efficiently.

2. Introduction

Over the last few decades, the objective of much robotics research has been to develop lightweight, autonomous flying robots that can navigate through cluttered and dynamic environments. Applications for these aircraft are numerous, including natural disaster monitoring, mapping, homeland security and search-and-rescue missions. Despite the vast engineering effort that has been focussed on this area, the realisation of such aircraft has remained elusive. One of the major challenges has been the development of a control system that is capable of flying through cluttered and ever-changing environments whilst being both lightweight and energy efficient.

Insects such as honeybees^{2,5}, bumblebees^{6,7} and flies^{8,9} employ simple, yet highly effective strategies for controlling flight that rely primarily on visual information. Although previous studies have been important for understanding insect flight control, they have, to date, relied almost exclusively on data from behavioural studies conducted in static, uncluttered environments under bright light conditions. To gain a better understanding of how more challenging visual habitats affect flight control strategies and visual systems, it is not only ideal to perform more detailed studies on the effect of varying the complexity of the environment, it is also necessary to perform investigations on insects that have evolved in more complex habitats, such as rainforests. Furthermore, comparative studies between insects that have evolved in environments of different complexity can reveal much about the behavioural and anatomical specialisations required for each situation. For such studies, the bumblebee and the orchid bee represent perfect model systems. While bumblebees are more adapted to navigating over open, meadow-like habitats, orchid bees are capable of navigating over long distances¹ in the ever-changing environment of the tropical rainforest. To achieve this, orchid bees have evolved flight control strategies that allow them to overcome the challenges of flight in a complex habitat, despite the restrictions imposed upon them by their small sensory systems and the limited processing power of their miniature brains.

To investigate the strategies and specialisations that allow flying insects to navigate in complex environments, we divided the project into two main themes: 1) Behavioural analyses of visually

guided flight control and 2) Anatomical analyses of the eye design and visual specialisations of flying insects. In Theme 1, we performed behavioural analyses of the flight control behaviours of various flying insects in order to elucidate differences or similarities in their flight control behaviour when negotiating clutter. In Theme 2, we performed high-resolution 3D analyses of the visual systems of the different model animals used in Theme 1 to better understand the sensory input that drives their flight control behaviour.

3. Methods, Assumptions and Procedures

Theme 1: Behavioural analyses of orchid bee flight control

Summary To fly through the rainforest, orchid bees must continuously negotiate small openings in the dense vegetation, something that they do with precision and at high speed. Do orchid bees employ a strategy that allows them to determine the safest point for passing through small openings, i.e. flying through the point that provides them with the greatest clearance? If this is the case, what information do they use to determine this point? To investigate the strategy that orchid bees use to negotiate apertures, we filmed bees flying through apertures of known size and dimension. The apertures differed in size and shape so that, in some cases, their geometrical centre was not coincident with the point of maximum clearance.

Do flying insects that live in complex environments use the same flight control strategies as those that fly in less cluttered habitats? The challenges of flight control for orchid bees are two-fold; not only must they control flight in the dim conditions of the understory of the tropical rainforest, they must also detect and avoid obstacles while navigating through this environment. Have orchid bees evolved different strategies for obstacle avoidance and flight control in order to cope with their habitat? If so, are these strategies more reliable in cluttered and dynamic environments than those employed by other insects? To answer these questions, we presented bumblebees and wasps, which are active in relatively open, bright habitats, with the same apertures that we presented to the orchid bees. By including comparisons between orchid bees and bumblebees, we were able to develop a thorough understanding of how light level and physical environment shape and limit the performance of visually guided flight control behaviour.

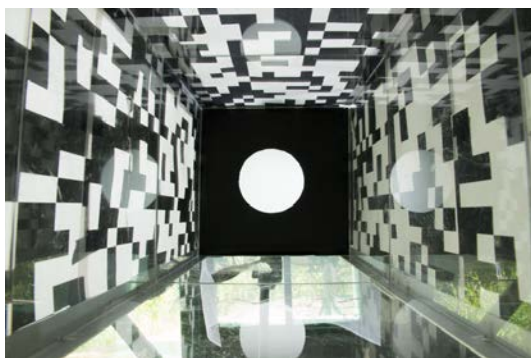


Fig. 1: The view from inside the experimental setup used to investigate the flight control strategies that flying insects use to negotiate apertures.

Setup We used a pair of synchronised high-speed cameras to record the flight trajectories of bees negotiating apertures of different sizes and geometries. The experimental setup consisted of a Perspex chamber, 300 mm high, 300 mm wide and 750 mm long (Fig. 1). The outer surface of the walls and roof of the chamber were covered in a randomized black and white (in equal proportions) 10mm x 10mm check pattern printed on semi-diffuse paper, which provided strong visual cues for flight control and allowed diffuse light to enter the experimental chamber. The floor of the chamber was left uncovered for observation. The back wall

was made of 5mm thick matte black foam board and was covered on the inside by the check pattern. The front wall of the chamber was constructed from matte black foam board (5mm thick) into which the different apertures were cut. Insects were captured and released into the back of the chamber. Their position when exiting the chamber through the aperture, or when crashing into the diffuser that was used to remove motion parallax cues (that is, the relative movement of the edges against the background) was recorded.

Theme 2: Anatomical and physiological analyses of the orchid bee visual system

Summary Does the visual system of orchid bees have specialisations that allow them to better use the visual information available in the rainforest? To gain an understanding of the information that the eyes receive, we performed a series of anatomical investigations of both the compound eyes and ocelli of orchid bees as well as a number of other tropical and temperate bee species for comparison. This work was done in collaboration with Prof. Willi Ribi at the University of Tübingen in Germany and Prof. Eric Warrant at Lund University in Sweden.

Detail We used traditional histological analyses, combined with light and electron microscopy to examine the internal structure and features of each visual system. We also created replicas of the compound eyes using nail polish, which allowed us to count the number of facets and to calculate how facet size (a proxy for resolution) changes across the eye. In addition, we developed a method for generating 3D models of bee eyes using x-ray micro computed tomography at synchrotron light sources in Switzerland and the UK. To understand how light was focussed by the lens onto the retina, we also developed a mathematical ray-tracing technique that was applied to the 3D volumes of the eyes. All of the 3D tomography and reconstruction techniques, as well as the ray-tracing method were developed primarily by the post-doc, Dr. Gavin Taylor, who was employed using the funding provided for this project. For further details of the analyses that we developed, please see the attached paper ‘The dual function of orchid bee ocelli as revealed by x-ray microtomography’.

4. Results and Discussion

Theme 1: Behavioural analyses of orchid bee flight control

To fly through the rainforest, orchid bees must continuously negotiate small openings in the dense vegetation, something that they do with precision and at high speed. Research on honeybees and bumblebees has shown that, to avoid collisions with the walls when flying along a corridor, they keep the rate of image motion (the movement of the visual scene across the eye) constant in each eye^{5, 10}. This has the advantage that the animal always keeps an equal distance between itself and nearby surfaces. A prediction of this behaviour is that, when presented with a circular aperture, the bees will fly closer to the centre. To begin with, we presented the bees with circular apertures of different sizes. We found that, when flying through these apertures, orchid bees would position themselves close to the centre and that the average

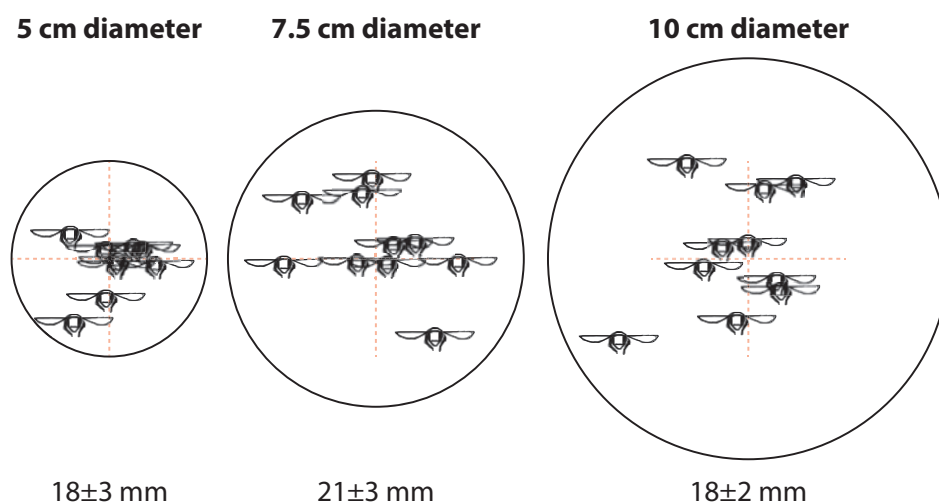


Fig. 2: Examples of how orchid bees positioned themselves when negotiating a circular gap of 5, 7.5 and 10 cm diameter. Values describe the mean \pm standard deviation of the distance between the bee's position and the centre of the circle for 20 flights in each circle.

distance to the centre was not affected by the width of the aperture when the diameters ranged from 5 cm to 10 cm (Fig. 2). Interestingly, the bees would not fly through a hole that was 2.5 cm in diameter, suggesting that they can, in some way, estimate the size of apertures. The results from this experiment indicate that the bees are indeed behaving as would be predicted if they were using an image motion-based strategy to control their position when flying through apertures.

To investigate how the performance of the orchid bees compared to the performance of other insects, we then presented the 10 cm diameter circle to bumblebees and wasps (Fig. 3). In this experiment, we found that both bumblebees and wasps were less accurate at flying through the centre of the circle. This result could be interpreted in two ways, firstly that bumblebees and wasps are not as accurate when flying through gaps or that they have a different strategy that perhaps does not entail flying through the centre of them.

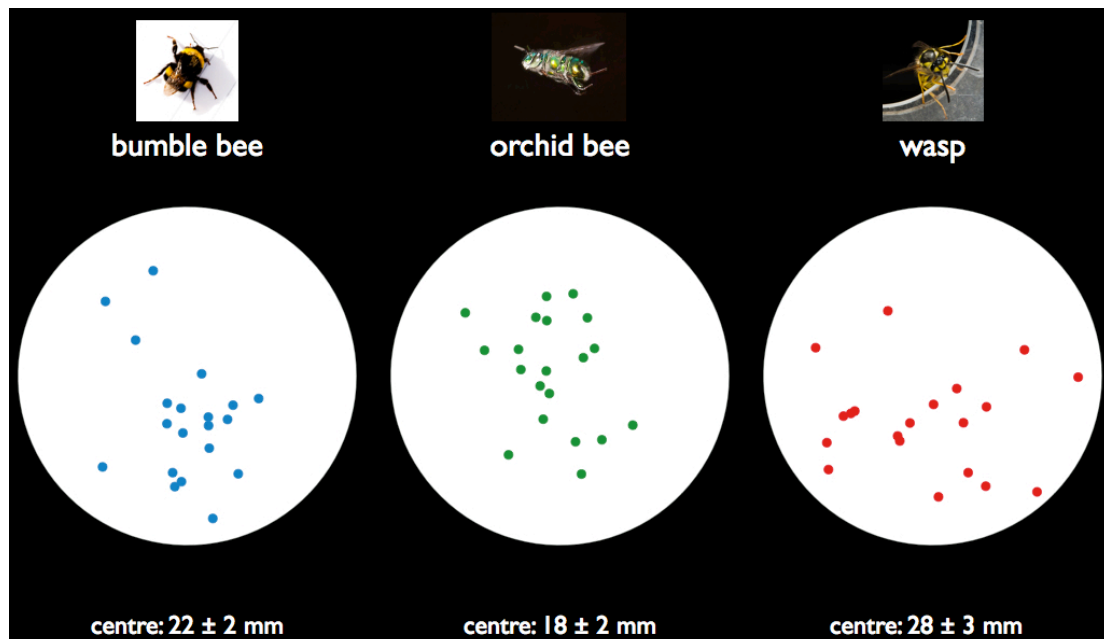


Fig. 3: The position of bumblebees, orchid bees and wasps when negotiating a circular aperture 10 cm in diameter. Values describe the mean \pm standard deviation of the distance between the position and the centre of the circle for 20 flights in each circle.

To investigate what strategies these insects might be using to negotiate the apertures, we presented these three species with an asymmetrical hole whose geometrical centre is not aligned with the point of greatest clearance (Fig. 4). The results of this experiment show that, while orchid bees tend to fly close to the point of greatest clearance, bumblebees and wasps do not (Fig. 5).

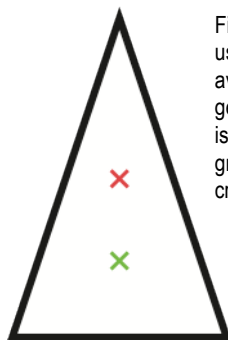


Fig. 4: The asymmetrical hole used to test obstacle avoidance in orchid bees. The geometric centre (red cross) is not the same as the point of greatest clearance (green cross).

This finding suggests that bumblebees and wasps have different strategies for negotiating apertures. It is possible that, due to the complexity of their rainforest habitat, orchid bees have developed more accurate or effective methods for flying safely through gaps than species from less complex environments.

This result was also supported by a series of experiments (performed by Klara Abrahamsson who received her Masters degree as part of this project) in which we recorded the number of individuals that were able to negotiate an aperture within a time period of 2.5 min. Over 3 orders of magnitude decrease in light intensity (1000-0), 100% (18/18) of orchid bees were still able to negotiate a 13 cm diameter circular aperture. In contrast, the number of bumblebees negotiating the aperture within the time period decreased dramatically with light intensity, from 95% at 120 lux to 40% at 6 lux ($n=24$). These findings suggest that the orchid bees' strategy for negotiating apertures is not affected by large changes in light intensity but that the bumblebee's ability to negotiate apertures suffers considerably in dim light.

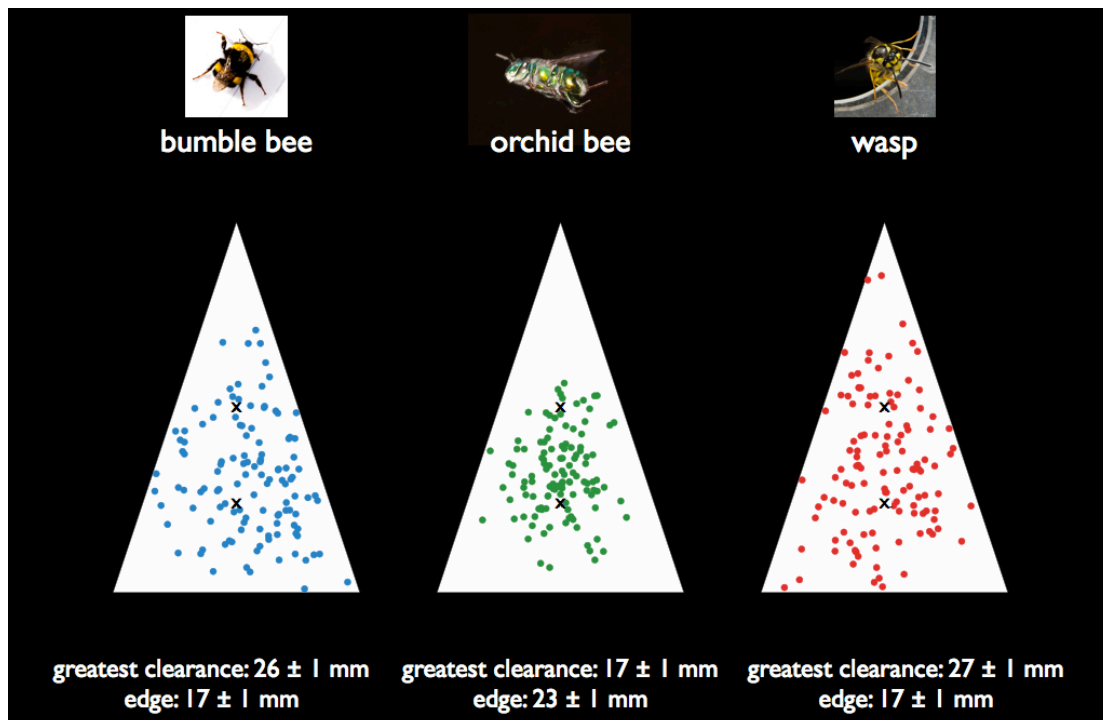


Fig. 5: The position of bumblebees, orchid bees and wasps when flying through a triangle aperture 15 cm high and 10 cm wide. Values describe the mean \pm standard deviation of the distance between the position and the point of greatest clearance or the edge of the aperture, $n = 120$ for each species.

The following is a summary of published findings (for more details please refer to the attached paper *Finding the gap: A brightness-based strategy for guidance in cluttered environments*). To investigate if orchid bees did use an image motion-based strategy for locating the point of greatest clearance when flying through an aperture, we filmed their flights when exiting the aperture and reconstructed the trajectories in 3D using synchronised high-speed cameras. We performed a series of mathematical calculations to identify the flight paths that we would predict if the bees were using an image motion-based strategy. This analysis showed that the bees would only be able to locate and fly through the centre of a circular aperture if their approach was perpendicular to the plane of the aperture and directed towards its centre. Our analysis of the flight trajectories revealed that, while the bees are indeed capable of flying towards the centre of a circular aperture, they do not necessarily approach it perpendicular to its plane. This result suggests that orchid bees do not use an image motion-based strategy for locating the centre of an aperture. We next performed a series of experiments using apertures of different shapes and sizes and found that, instead of using an image motion-based strategy to guide them through apertures, orchid bees actually use brightness cues. This strategy works because the brightest part of an aperture is always located on the point that provides greatest clearance from its edges. Furthermore, we found that the bees used brightness cues to determine if an aperture was sufficiently large to negotiate (this explains our earlier finding that they would not fly through a circular aperture of 2.5 cm diameter). This use of brightness cues as a simple fast and efficient guidance strategy is one of the most significant and novel findings of this project.

Theme 2: Anatomical and physiological analyses of the orchid bee visual system

Compound eye morphology We began our investigation into the compound eye morphology of orchid bees using a nail-polish replica technique that allowed us to recreate a so-called ‘eye map’. This eye map gives us information about the number of ommatidia, as well as their size (which can be used as a proxy for resolution. Interestingly, when we compared the eye map of the orchid bee with that of a bumblebee with a similar-sized head (Fig. 6), we see some extraordinary differences in both facet number (orchid bees have about 10 000 facets compared to the 6 000 of a bumblebee with a similarly, sized head) and facet size, orchid bees have much larger facets than bumblebees.

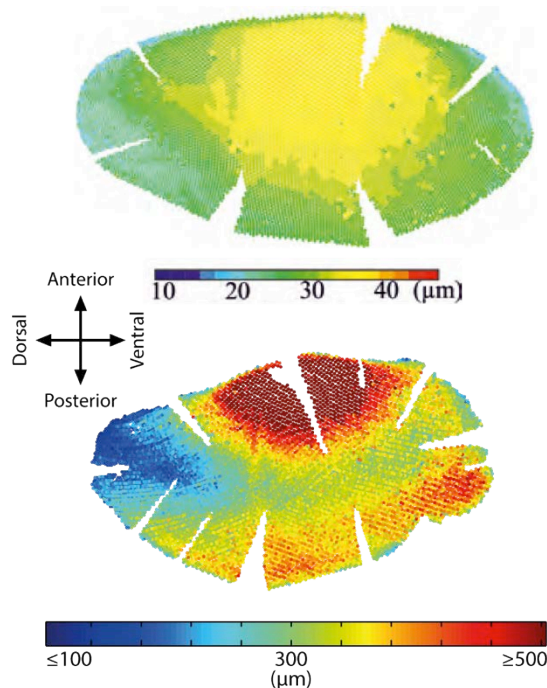


Fig. 6: Ommatidial size maps of a bumblebee (top, reproduced from Streinzer et al. 2014 PLoS One) and a tropical orchid bee with a similar eye size. Scales for the heat maps are shown below each eye. Areas of potential high resolution are shown with yellow/red colours. The two areas of unusually high resolution in the front and back regions of the orchid bee eye are shown in red.

Preliminary analyses using standard microscopy techniques have suggested that tropical bees do indeed have some extraordinary visual specialisations. In the compound eye, ommatidial size maps (a proxy for visual resolution, Fig. 5) suggest that tropical bees may have a unique backwards-facing area of high resolution. To investigate this in more detail, we performed high resolution micro-computed tomography (micro-CT) at synchrotron light sources in Switzerland and the United Kingdom. This has allowed us to develop 3D models of the compound eyes (Fig. 7). We are currently working on an automated method for extracting information about the size and position of each facet in space from the models and we expect this to be finished by the end of 2016. However, our preliminary analyses already give us an indication that the area of large facets at the back of the orchid bee eye is located on a relatively flat surface (Fig. 8), lending further support to the hypothesis that this represents an area of backward-facing high resolution. Understanding what the bees might use this for is the topic of ongoing investigations.

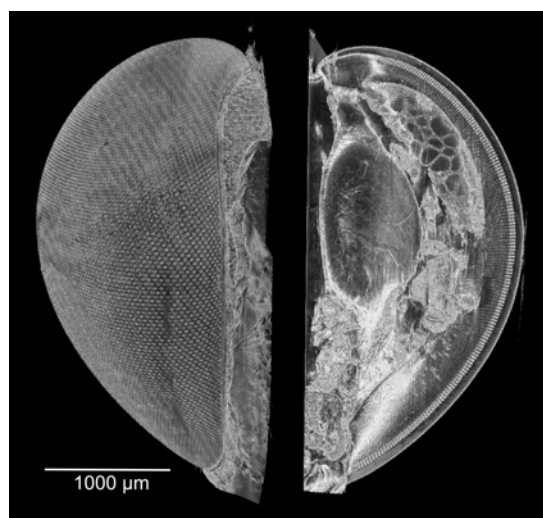


Fig. 7: A 3D model of an orchid bee compound eye created from a micro-CT scan taken at a synchrotron light source.

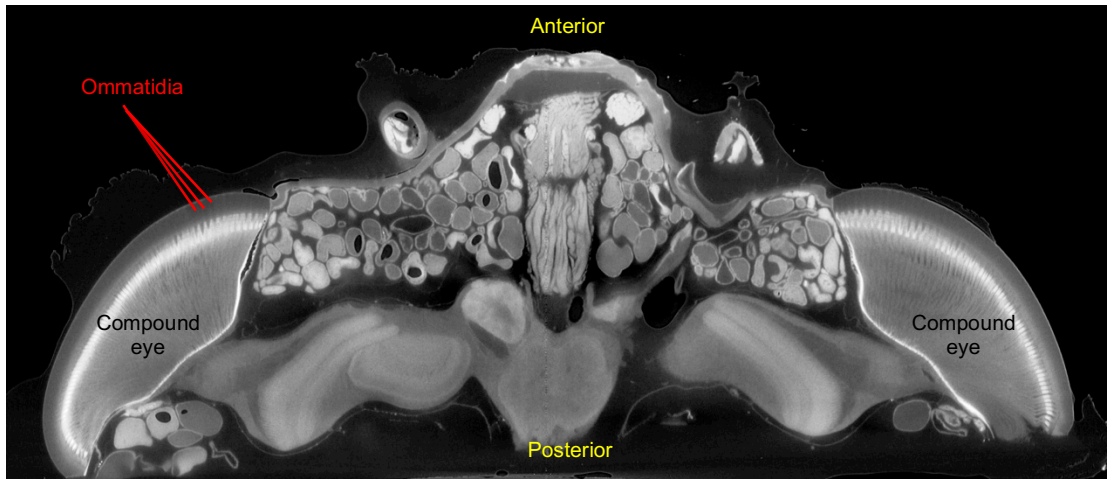


Fig. 8: A micro-CT scan of an orchid bee head showing the compound eyes and ommatidia. Note the relatively flat region towards the back of the eye (towards the lower edge of the image).

In addition to taking scans of the orchid bee compound eyes, we have also taken over 50 scans of the compound eyes of around 15 other tropical and temperate bee species. Our future goal is to compare the morphology of the compound eyes across species and habitat to determine what features tropical bees have evolved in order to cope with flight and navigation in their complex habitat.

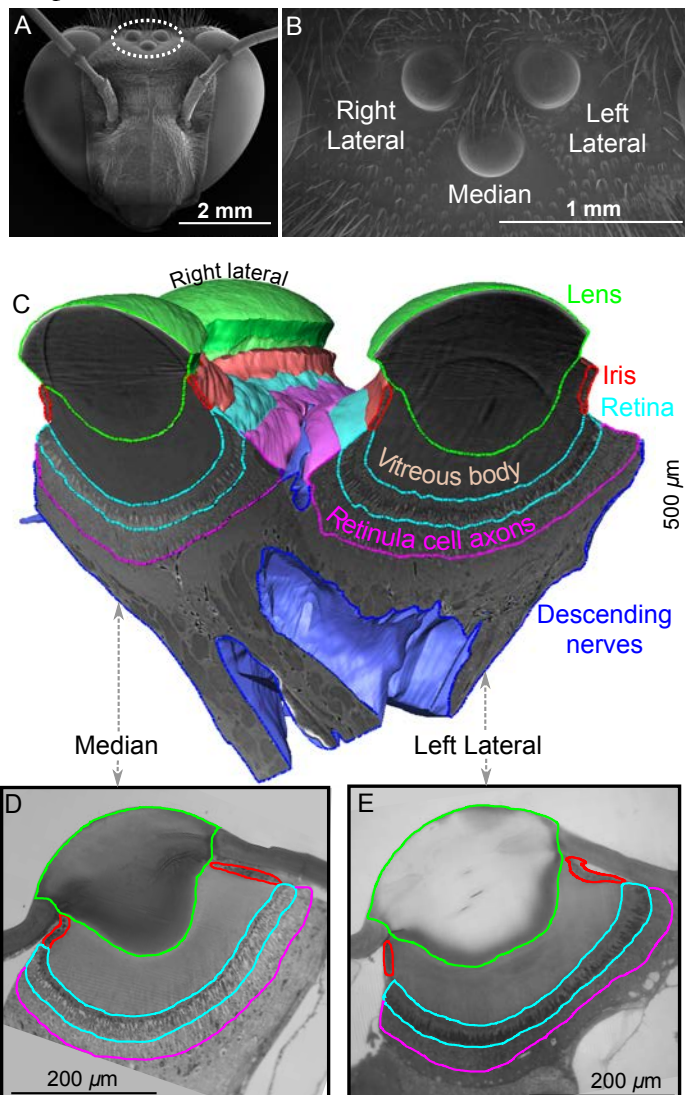


Fig. 9: Orchid bee ocellar morphology. **A-B** SEM images of the orchid bee head and ocelli. **C** A 3D model of the ocelli reconstructed from micro-CT. **D-E** Histological sections through the ocelli showing the same features as in C.

Ocellar morphology

In combination, our histological and micro-CT analyses of the unusually large simple eyes (or ocelli) of orchid bees reveal that they have some unusual features (Fig. 9). These include a large 'clear zone' or vitreous body between the lens and the underlying retina (Fig. 8C-E). This is unusual because the ocellar retinæ of most insects investigated to date sit directly behind the retina. To understand what effect this large zone has on the image that is formed on the retina, we developed 3D models of the ocelli from micro-CT analyses and then performed optical ray-tracing simulations on the models to determine the shape and position of their visual fields. Surprisingly, we found that each ocellus possessed two distinct visual fields; each has a focused *monocular* visual field suitable for detecting features elevated slightly above the horizon and therefore potentially assisting with flight stabilization and, unlike several other ocelli investigated to date, a large frontally to dorsally oriented visual field shared by all three ocelli. Detailed histological analyses showed that photoreceptors in the ocellar

retinae are likely to be sensitive to the polarization of light, and, while they have similar orientations within each ocellus, the average orientation is offset by approximately 40° in each eye. Unlike in any other insect eye described to date, these ocelli meet the requirements of a true polarization analyser – three units with different directions of polarization sensitivity viewing the same region of space. The ocelli of *E. imperialis* could thus provide sensitive compass information for navigation in low light conditions, and additionally, provide robust, intensity invariant, visual cues for visual discrimination or flight control. This work provides a major advance in our understanding of ocellar functions. For further details, please see the attached paper ‘The dual function of orchid bee ocelli as revealed by x-ray microtomography’.

In addition to the 3D models of the orchid bee ocelli, we have developed 3D models of other tropical and temperate bee species. We are currently working on analysing the data from these models so that they can be compared with the features of the orchid bee ocelli to provide us with new insights into the visual specialisations necessary for guidance in tropical and temperate environments.

5. Conclusions

The most significant outcomes of this three-year AFOSR funded project have been the discovery of a novel guidance strategy for cluttered environments, the development of state-of-the-art techniques for acquiring and analysing data from 3D models of eyes and, through them, the discovery that the ocelli of orchid bees have more than one function. These breakthroughs are not only relevant to our understanding of how orchid bees navigate through a rainforest environment, but also for our understanding of the optimal visual strategies and specialisations for navigation in cluttered environments. This has direct importance for the design and development of lightweight, energy efficient guidance systems that will allow autonomous robots to move through clutter without the need of active sensors such as laser, sonar or GPS. The methods that we have developed during the course of this project and the data that we have acquired has led to the publication of two published papers in highly ranked scientific journals and at least four related papers are in preparation. These methods are not only directly useful for this project but are likely to become the cornerstone of vision research in the future as they provide unprecedented detail about how animals actually perceive the world and, in turn, the specialisations that they have developed to help them survive in different environments.

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